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MORPHOLOGICAL AND VOCAL VARIATION ACROSS A CONTACT ZONE BETWEEN THE CHICKADEES *PARUS ATRICAPILLUS* AND *P. CAROLINENSIS*

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ABSTRACT.—A contact zone between Black-capped and Carolina chickadees (*Parus atricapillus* and *P. carolinensis*) exists in southwestern Missouri. It was less than 15 km wide and paralleled the interface between the relatively treeless Great Plains and the forested Ozark Plateau. Many birds in this zone were intermediate in morphology or vocalizations or both. Moreover, both morphological and vocal discriminant analysis scores of contact zone birds were unimodally distributed and there was no correlation between morphological discriminant scores of mated males and females in the contact zone, indicating little or no assortative mating. Playback experiments demonstrated that birds to the north or south of the contact zone responded aggressively only to their own song type, while contact zone birds responded to either song type. We believe that southwestern Missouri contact zone populations are derived from extensive hybridization between *atricapillus* and *carolinensis*. *Received 26 August 1985, accepted 28 March 1986.*

NARROW contact zones represent a common pattern of geographic variation in living organisms (Remington 1968). These zones traditionally have been believed to represent intermediate stages in the process of species formation (Mayr 1963). Recent investigators have given more credence to the possibility that some contact zones may represent a stable form of geographic variation and need not always result in speciation or extinction of one form (Moore 1977). The development of quantitative genetic models of clinal variation (May et al. 1975, Endler 1977) demonstrates that, given appropriate levels of gene flow and natural selection, clines of any configuration (including narrow contact zones) can be established and maintained indefinitely with or without secondary contact. Thus, narrow contact zones may also represent a limiting case in the spectrum of normal patterns of geographic variation. Hence, the study of contact zones may shed light on a variety of microevolutionary processes ranging from cline formation to speciation.

To understand the interactions occurring at a particular contact zone, it is essential to have an adequate measure of genetic introgression across it. A variety of evidence must be examined, because the extent of introgression indicated by a single data set may be misleading.

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Several studies have found introgression at the protein level to be much more pervasive than introgression of morphological or behavioral characteristics (Dessauer et al. 1962, McDonnell et al. 1978, Braun 1983). In other cases, where hybridization was suspected on morphological criteria, molecular evidence showed that little introgression had occurred (Duncan and Highton 1979, Lawson and Dessauer 1979, Schwaner et al. 1980). Among birds, song type is a commonly used, though often nongenetic, measure of introgression between populations. Introgression of song type apparently has outstripped morphological introgression in some cases (Emlen et al. 1975), while in others the opposite appears to be true (Braun 1983).

In this and a related study (Braun and Robbins 1986), morphological, behavioral, and molecular evidence was gathered to clarify the extent of genetic introgression across a narrow contact zone involving the Black-capped and Carolina chickadees (*Parus atricapillus* and *P. carolinensis*). These two forms are distributed parapatrically across eastern North America. They come together in a narrow contact zone that stretches from New Jersey to Kansas, dipping southward in the Allegheny Mountains of Pennsylvania and West Virginia (Brewer 1963). From eastern Illinois across Indiana, however, the two forms are separated by a narrow gap (Brewer 1963, Merritt 1981). An analogous situation prevails in the Great Smoky Mountains of southern Appalachia. Here, breeding populations of *atricapillus* and *carolinensis* are separated by an altitudinal gap of about 180 m (Tanner 1952).

Although some hybridization has been suspected in the contact zone (Brewer 1963, Rising 1968, Johnston 1971, Ward and Ward 1974, Merritt 1978), some problems beset the accurate assessment of hybridization between these two forms. First, there is some overlap in all morphological characters yet analyzed. Thus, individuals can be exceedingly difficult to classify, and satisfactory identification of hybrids based on morphological characters requires multivariate statistical methods (Rising 1968, James and Rising in press). Second, although the two forms have distinctive songs, the extent to which song type is determined genetically is not known in this complex. Birds from the contact zone that sing intermediate or aberrant songs usually are considered hybrids (Brewer 1963, Johnston 1971). However, the possibility of vocal mimicry or heterospecific song learning has not been eliminated (Ward and Ward 1974). Third, not all studies have focused on local chickadee populations during the breeding season. This results in uncertainty as to how migrant or wandering birds might affect the apparent frequency of hybridization (Rising 1968). Because of these difficulties, the extent of genetic interaction between *P. atricapillus* and *P. carolinensis* is still poorly known.

MATERIALS AND METHODS

Fieldwork and study sites.—Preliminary fieldwork was conducted in southwestern Missouri during March–May 1975, April 1977, and April 1978 to delineate the ranges of the two forms and the position of the contact zone. A locality was considered to be in the contact zone if any bird at the site demonstrated vocal intermediacy (i.e. sang intermediate songs, aberrant songs, or both song types) or morphological intermediacy (in plumage color characters). Classification of localities was based on 1–6 birds per site. Locally breeding populations were studied intensively during March–April 1980 at four sites in St. Clair and Bates counties along a transect of the contact zone (sites 1–4 in Fig. 1). Samples of 15 or more individuals per locality were collected. A series of 18 *atricapillus,* collected in April 1979 in northwestern Missouri (Nodaway Co.), also was used in the morphological analysis. All specimens were deposited at the Louisiana State University Museum of Zoology.

Formerly, the native vegetation of the northern and western sections of the study area (Fig. 1) was tall-grass prairie, with forest restricted primarily to watercourses (Schroeder 1981). The eastern section, which is on the Ozark Plateau, was covered with an oak-hickory association. Today, the entire area is heavily cultivated, with most forest restricted to riparian areas and isolated woodlots. More forest remains in the eastern section of the study area because of unfavorable soil conditions for cultivation on the Ozark Plateau.

Morphological analysis.—Specimens were weighed to the nearest 0.1 g (0.5 g for some populations). Wing length (chord) and tail length (insertion to tip of longest feather) were measured to the nearest 0.1 mm with dial calipers. All specimens were taken in late March through early May so they were homogeneous with respect to molt and feather wear. Specimens with extensive wear were eliminated from the analysis. This reduced the usable sample size considerably for some populations. Bivariate plots of wing vs. tail, wing vs. mass, and tail vs. mass showed no consistent variation between sexes; therefore, we pooled males and females within each population

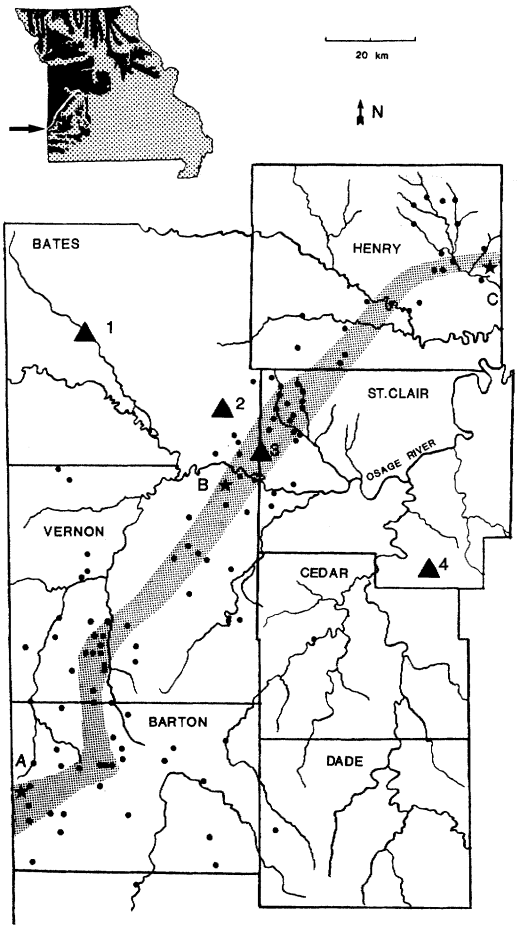

Fig. 1. Chickadee contact zone in southwestern Missouri. Solid circles represent localities where 1–6 chickadees were heard. Shaded region includes all localities where mixed or aberrant song repertoires were recorded. Only *P. atricapillus* songs were heard north and west of the shaded area, and only *P. carolinensis* songs were heard to the south and east. Geographic reference points within the contact zone are marked by the stars labeled (A) Mindenmines, (B) Schell-Osage Wildlife Management Area, and (C) Roseland. Large triangles represent sites intensively studied on a transect of the contact zone. Site 1: 5 km north and 8–13 km west of Butler. Site 2: 6.5 km north and 4 km west of Rockville. Site 3: 1.5 km east of Rockville. Site 4: 6.5 km west of Collins. Inset map of Missouri depicts chickadee contact zone in relation to prairie (black) and forest (stippled) vegetation in presettlement Missouri. The chickadee contact zone is superimposed in white, beginning with the arrow at the southwestern edge of the state. It continues northeastward paralleling the forest-plains ecotone. The zone is shown only as far as we have determined its exact position. Inset map modified from Kucera

sample. Because females are significantly smaller than males, female measurements were adjusted by adding to each female value the difference between the male and female mean values for its population sample.

A discriminant analysis was performed on the morphological data set using the program of Veldman (1967). Initially, reference samples of 16 *atricapillus* (7 from Nodaway Co., 9 from Site 1) and 15 *carolinensis* (Site 4) were used to derive a single discriminant function that produced maximal separation between these samples on the basis of mass, wing length, and tail length. This function was evaluated to yield discriminant scores for each individual in the reference samples, as well as in the contact zone. Discriminant weighting coefficients for each variable are given in Table 1.

Analysis of vocalizations.—Chickadee songs were recorded on a Uher CR-240 cassette recorder with a Sennheiser ME-88 shotgun microphone. We collected as many tape-recorded birds as possible for morphological comparisons. The propensity of chickadees to sing varied greatly with weather conditions, however, so vocalizations of all populations were not sampled equally (see below). Recordings were analyzed on a Kay Sona-Graph (Model 6061A) with the narrow band (45 Hz) filter. Spectrograms were made of every song type recorded from each bird. The sole criterion used in distinguishing song types was the number of notes per song. We made spectrograms of five repetitions of each song type from each individual. In those cases in which a bird repeated a particular song type less than five times, we made spectrograms of all repetitions available.

Eight measurements were made on each spectrogram: duration of the first note; duration of the second note; onset, midpoint, and offset frequency of the first note; and onset, midpoint, and offset frequency of the second note. For each individual, we computed the mean value of each measurement across repetitions of a song type. For birds that sang more than one song type, each song type was treated as a separate song bout. Mean values of the measurements for each bout from each bird were entered as the raw data in a discriminant analysis designed to produce maximal separation between reference groups of 14 *atricapillus* bouts (5 from Site 1, 9 from Site 2) and 15 *carolinensis* bouts (Site 4). Discriminant weighting coefficients produced by the computer analysis are shown in Table 2. The discriminant function was then evaluated to yield a discriminant score

←

(1961) and Schroeder (1981). Sections of eastern Henry Co. surveyed in 1975, 1977, and 1978 have since been flooded due to creation of the H. S. Truman dam.

TABLE 1. Morphological measurements of Missouri chickadee samples.

Population	Sex	*n*	Mass (g)	*n*	Wing length (mm)	*n*	Tail length (mm)	*n*	Tail/wing ratio
Parus atricapillus									
Nodaway Co.	M	12	13.6 ± 0.7	13	67.5 ± 1.9	8	61.9 ± 2.3	8	0.93 ± 0.03
	F	6	12.7 ± 0.7	6	64.2 ± 1.9	3	59.7 ± 1.2	3	0.93 ± 0.01
Site 1	M	9	13.3 ± 0.7	9	66.1 ± 1.6	4	62.3 ± 0.6	4	0.95 ± 0.01
	F	8	12.3 ± 0.8	8	62.9 ± 1.1	5	60.7 ± 1.6	5	0.96 ± 0.02
Site 2	M	8	13.6 ± 0.8	7	66.4 ± 1.8	5	62.7 ± 2.7	5	0.95 ± 0.02
	F	6	12.0 ± 1.1	6	62.1 ± 1.6	4	58.9 ± 3.6	4	0.94 ± 0.04
Contact zone									
Site 3	M	32	12.0 ± 0.8	34	65.6 ± 2.0	33	58.7 ± 2.3	33	0.90 ± 0.03
	F	10	11.5 ± 0.8	9	61.8 ± 2.6	9	55.9 ± 5.0	9	0.90 ± 0.05
Parus carolinensis									
Site 4	M	12	11.5 ± 0.6	12	63.7 ± 1.1	8	55.6 ± 1.2	8	0.87 ± 0.02
	F	8	10.8 ± 0.6	7	60.3 ± 0.8	5	53.0 ± 1.1	5	0.88 ± 0.01
Discriminant function weighting coefficients (unstandardized)			0.7944		0.0502		0.6053		

for each bout in the reference groups, as well as the 51 bouts from the contact zone.

Playback experiments.—At each site visited in 1980, playback experiments were carried out to test the response of each population to both song types. A master tape with 2 min of the song of each form was used in all experiments. Typically, we located a pair by their calls or observed them foraging quietly. We first played 2 min of the song type to which we least expected them to respond, waited 2 min, then played 2 min of the song to which we most expected them to respond. For example, if most birds in an area sang *atricapillus* songs, we first played *carolinensis* song, waited 2 min, then played *atricapillus* song. If a bird seemed to respond to the first song type played, we often stopped the tape, let the bird calm down, then tried the first song type again to verify its response. We noted the nature and intensity of each response and attempted to tape a representative sample of song from all singing birds. We collected as many of the birds as possible for morphological characterization. Playback results were based only on the response of singing individuals, i.e. females that accompanied responding males were not tallied, with the exception of three females that sang.

RESULTS

Distribution of chickadees in Missouri.—Based on song types and morphology of birds from 113 localities in a seven-county area, the ranges of the two chickadees abut from near Mindenmines, Barton Co., through Schell-Osage Wildlife Area, Vernon Co., to near Roseland, Henry Co. (Fig. 1). A narrow contact zone, less than 15 km wide at the widest point, separates the two forms. This contact zone closely parallels the interface between the forested Ozark Plateau and the largely treeless Great Plains throughout the study area (Fig. 1). The chickadee contact zone does not coincide exactly with the ecotone but appears to be displaced several kilometers onto the plains all along its length (Fig. 1).

Morphological comparisons.—*Parus atricapillus* samples averaged larger than *carolinensis* in mass, wing length, and tail length, while the contact zone sample was intermediate in all measurements (Table 1). However, the various populations overlapped broadly in these measurements. Samples of *atricapillus* also averaged higher than *carolinensis* in the ratio of tail length to wing length (Table 1), the statistic most commonly used to separate these two forms. The contact zone sample was intermediate in tail/wing ratio, and the sample distribution showed no evidence of bimodality (Braun 1983). A bimodal distribution would be expected if assortative mating were common in the zone.

Better separation between samples was achieved by a multivariate discriminant analysis of mass, wing length, and tail length (Fig. 2). The reference sample of *atricapillus* received high discriminant scores and *carolinensis* low ones. The contact zone sample had intermediate discriminant scores with a markedly in-

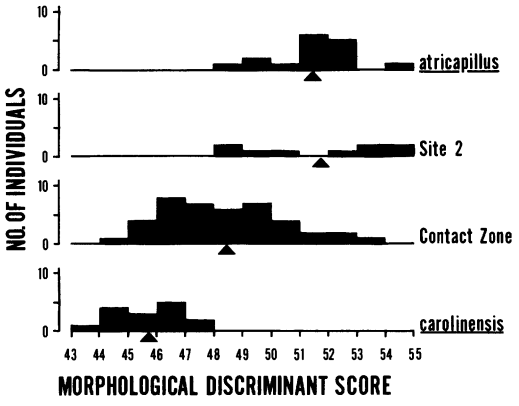

Fig. 2. Distribution of morphological discriminant scores in chickadee population samples. *atricapillus*: reference sample of 16 birds (7 from Nodaway Co., northwestern Missouri; 9 from Site 1) used in deriving discriminant function. Site 2: 9 birds from Site 2. Contact zone: 42 birds from Site 3. *carolinensis*: reference sample of 15 birds from Site 4 used in deriving discriminant function.

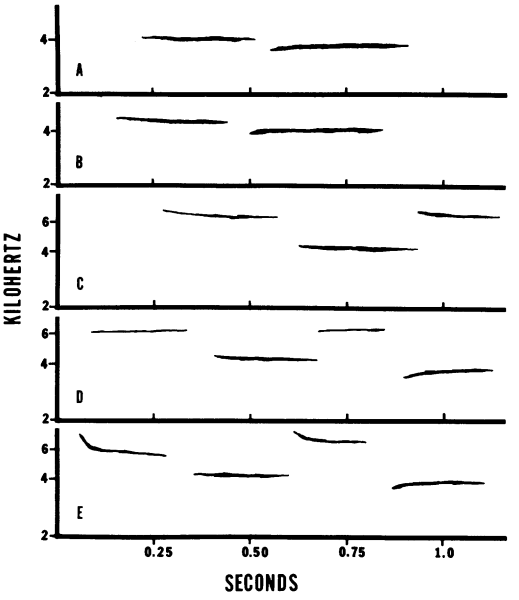

Fig. 3. Tracings of spectrograms of Missouri chickadee vocalizations. Kilohertz scale is logarithmic. (A) *P. atricapillus* song from Site 1. (B–D) Two-noted, three-noted, and four-noted songs of a single contact zone individual from Site 3. (E) *P. carolinensis* song from Site 4.

creased range and standard deviation from the mean (Table 1). Like the tail/wing ratio, the distribution of contact zone discriminant scores showed no evidence of bimodality (Fig. 2).

We sought further evidence on the occurrence of assortative mating in the contact zone by comparing the morphological discriminant scores of mated pairs. If birds tended to choose mates morphologically like themselves, there should be a correlation between the discriminant scores of mated individuals. In fact, a linear regression analysis of scores from the nine mated pairs for which we had complete data revealed no significant relationship between male and female scores ($r = 0.101$; not significant). We are confident that these individuals were actually mated pairs for several reasons. First, chickadee flocks had dispersed by late March when our studies began, and practically all chickadees were encountered singly or in pairs. Second, for many pairs, behavioral evidence that they were mated was observed, such as visitations to the same nest hole or common defense of a territory. Finally, all collected pairs that we believed to be mated ($n = 27$) in fact consisted of one male and one female.

Vocal comparisons.—The whistled song of *Parus atricapillus* is two-noted, while that of *P. carolinensis* is generally four-noted (Fig. 3). Considerable variability in song composition existed in the contact zone. Many individuals had a complex song repertoire consisting of *atricapillus*-like, *carolinensis*-like, and intermediate songs (e.g. Fig. 3). In southwestern Missouri, more than half of the contact zone birds we recorded sang more than one song type (15 of 29 individuals). This is sure to be a minimum estimate of the frequency of mixed repertoires because taping sessions with an individual often lasted only a few minutes, and we probably did not record the full repertoire of many birds.

The variation in these vocalizations was analyzed by measuring eight frequency and duration characteristics of each song (Table 2). For birds with multiple song types, each song type was treated separately, because averaging them would tend to bias contact zone values toward intermediacy. The reference sample means for each variable were different (Table 2), and in each case the mean for the contact zone sample fell between the reference sample means. This result could be obtained, however, even if only "pure" songs of the two types were averaged together in the contact zone sample. To demonstrate the extent to which individual song

TABLE 2. Measurements of song variables for Missouri chickadee samples.

	P. carolinensis	Contact zone	*P. atricapillus*	Discriminant function weighting coefficients (unstandardized)
No. of individuals	12	29	14	
Total no. of song bouts analyzed[a]	15	51[b]	14	
Duration of note 1 (msec)	126 ± 32	157 ± 32	204 ± 20	0.0237
Duration of note 2 (msec)	140 ± 18	173 ± 36	220 ± 24	0.0284
Onset frequency of note 1 (kHz)	6.71 ± 1.12	5.32 ± 1.28	4.18 ± 0.41	−0.4327
Midpoint frequency of note 1 (kHz)	5.96 ± 0.89	5.02 ± 1.19	3.91 ± 0.29	0.4138
Offset frequency of note 1 (kHz)	5.88 ± 0.86	4.97 ± 1.18	3.87 ± 0.30	−0.0464
Onset frequency of note 2 (kHz)	4.06 ± 0.49	3.75 ± 0.47	3.26 ± 0.27	0.2332
Midpoint frequency of note 2 (kHz)	4.09 ± 0.38	3.81 ± 0.34	3.46 ± 0.18	−0.6121
Offset frequency of note 2 (kHz)	4.09 ± 0.37	3.80 ± 0.33	3.48 ± 0.16	0.4571
Mean discriminant score	0.49 ± 0.11	1.04 ± 0.22[c]	1.27 ± 0.13	
		0.88 ± 0.25[d]		
		0.79 ± 0.21[e]		

[a] For individuals that sang more than one song type, each song type was treated as a separate song bout.
[b] 19 two-noted, 14 three-noted, and 18 four-noted song bouts.
[c] Two-noted bouts.
[d] Three-noted bouts.
[e] Four-noted bouts.

bouts were intermediate, data for the eight variables were subjected to a discriminant analysis. When individual discriminant scores for each song bout were plotted on a histogram (Fig. 4), the reference samples were well separated. Scores for 19 of 51 (37%) contact zone bouts fell in between the reference sample scores. The distribution of contact zone scores was unimodal, while the range of scores was increased greatly over the reference samples. Two, three, and four-noted song bouts in the intermediate range were common. There was only a minor tendency for two-noted or four-noted song bouts (ostensibly the parental song types) to group near the *carolinensis* or *atricapillus* reference sample, respectively. These data suggest that, within the zone, the number of notes in a song is a poor predictor of its duration and frequency characteristics. Although many songs recorded in the zone could be classified by number of notes as one or the other parental type, such songs were not necessarily accurate renditions of the parental song; they often showed subtle influences of the other song type.

We also examined the relationship between the vocal and morphological discriminant scores in contact zone birds for which we had complete data (Fig. 5). If a major proportion of contact zone birds were actually pure parental types (because of assortative mating or immigration into the zone), there should be a tendency for them to cluster about the parental means. In fact, practically every individual was intermediate in vocal score, morphological score, or both.

Playback experiments.—At Site 1, 10 chickadees responded only to *atricapillus* playback, while 2 exhibited no response. At Site 2, just 5 km northwest of the contact zone, we heard only typical *atricapillus* songs. Accordingly, 8 birds showed no interest in *carolinensis* songs broadcast in their territory, although they responded immediately to *atricapillus* tapes. Two Site 2 birds, however, gave weak or ambivalent responses to *carolinensis* songs. These responses included approach and intermittent singing of *atricapillus*-like song while foraging, but never the aggressive response expected for rival vocalizations. In the contact zone (Site 3), 11 individuals responded to both song types, 6 birds only to *atricapillus*, 6 only to *carolinensis*, and 3 exhibited no response. Morphological data were available for only 4 individuals that responded to only one song type in the contact zone. There was no apparent correlation between playback response and morphological affinities; the morphological discriminant scores

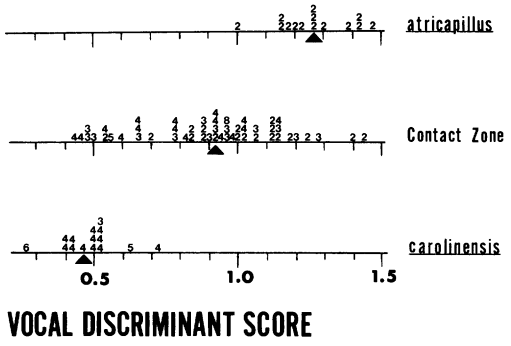

Fig. 4. Distribution of discriminant function scores based on 8 song variables in Missouri chickadee populations. The numerals refer to the number of notes in a song. Each numeral represents one song bout. *atricapillus*: reference sample from Sites 1 and 2. Contact zone: Site 3 sample. *carolinensis*: reference sample from Site 4.

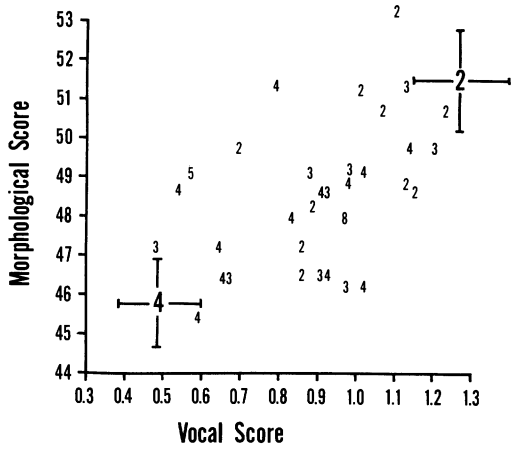

Fig. 5. Morphological and vocal discriminant scores for contact zone chickadees (Site 3). Numerals represent the number of notes in the bird's song type. For birds that sang more than one song type, each song type was treated separately. The large 2 and 4 with error bars mark the means and standard deviations of reference *P. atricapillus* and *P. carolinensis* samples, respectively.

of the 2 *atricapillus*-responding individuals were 49.04 and 51.22, while the scores of the 2 *carolinensis*-responders were 48.78 and 51.27. These scores are on the *atricapillus* side of the contact zone mean (Fig. 2). Finally, at Site 4, only 3 birds showed any response—all to *carolinensis*. This was the result of poor weather conditions. Nonetheless, in visits to this site prior to our intensive playback experiments in 1980, birds responded only to *carolinensis* song. These results demonstrated that the proclivity of chickadees to respond to a given song type was tied closely to the frequency of usage of that song type in the local population.

Discussion

Morphological comparisons.—Our morphological data confirm and extend the observations of Rising (1968) on chickadees in southeastern Kansas. Rising found morphological intermediacy in 15–50% of birds from the contact zone. This represented a minimum estimate of intermediacy because, as Rising recognized, his winter-collected sample might have included wandering birds from other populations. We found that some individuals in populations breeding in and near the contact zone in southwestern Missouri were strictly intermediate morphologically (i.e. falling in the range between reference sample scores), and that the distribution of contact zone scores was unimodal, with a mean about halfway between the reference means and range and standard deviation greatly increased over those of the reference samples. This distribution clearly suggests that the contact zone sample is derived through extensive interbreeding of *atricapillus* and *carolinensis*. Although some contact zone individuals fell within the range of the parental populations, it is to be expected that, even in a randomly mating hybrid population of chickadees, some individuals will approach parental morphology. The parental forms are so similar that many backcross hybrids might fall within the range of parental variation.

It is critical to sample locally breeding populations. Most studies of the chickadee contact zone have included nonbreeding populations. For example, Merritt (1978, 1981) captured, measured, and released 53 chickadees in winter at the range interface in Indiana. Only 2 of 30 *atricapillus* and 4–16 of 23 *carolinensis* were observed later in the study area during the breeding season. The disappearance of so many individuals probably indicates that some birds belonged to other than locally breeding populations (Merritt 1981). Many of the *atricapillus* may have been wintering birds from farther north. Merritt (1981) reported that 11 of these birds showed some intermediacy in morpho-

logical characters, suggesting that some hybridization occurs in this region. The extent of hybridization may have been masked by seasonal movements.

Evidence of genetic introgression across the range interface would be more important than simple morphological intermediacy in the contact zone. Hybridization in the zone might be common; but if selection against hybrids was intense, then gene flow across the zone could be restricted (Moore 1977). Our morphological data are probably inadequate to measure introgression between chickadee populations, both because the parental forms are so similar and because our data from sites just outside the contact zone (e.g. Site 2) were limited.

Another way to look at the question of introgression is to ask if there are selective factors in the environment that could stabilize the contact zone. An appropriate selection gradient might maintain a steep cline in morphological characters, leaving gene flow at other loci relatively unrestricted. It probably is not coincidental that the contact zone parallels a major ecotone, the interface between the forested Ozark Plateau and the largely treeless Great Plains. Remington (1968) identified this as a "suture zone," an area where many contact zones coincide, and this area is an ecotone between major biotic communities (Pitelka 1941, Kucera 1961). The ecological gradient in this area may provide selective pressure for the size-related characters that distinguish these chickadees. Actually, the ecological gradient only needs to produce a local steepening to an already well-marked ecogeographic cline. *Parus carolinensis* shows a strong tendency to be larger in the northern part of its range and smaller in the south, in accord with Bergmann's rule (James 1970). Size clines for *P. atricapillus* have not been analyzed in detail, but appear to conform to Bergmann's rule (see subspecies measurements in Ridgway 1904, Duvall 1945). Overall, we believe the available evidence on whether the contact zone actually impedes gene flow between *atricapillus* and *carolinensis* is equivocal at best.

Although the contact zone clearly parallels the forest-to-plains ecotone, it is displaced several kilometers onto the plains (Fig. 1). This displacement may be due to greater gene flow from the *carolinensis* side, where chickadee populations are larger because of the extensive forest habitat on the Ozark Plateau. The fact that the contact zone morphological discriminant scores were skewed toward *carolinensis* (Fig. 2) indicates a greater genetic contribution from that form.

Vocal comparisons.—Some degree of vocal intermediacy in chickadee populations from a number of contact areas has been reported (Tanner 1952, Brewer 1963, Johnston 1971, Ward and Ward 1974, Merritt 1981). We characterized chickadee songs quantitatively in an attempt to identify vocal intermediacy and showed extensive intermediacy in the songs of contact zone birds. Thirty-seven percent of all contact zone song bouts were strictly intermediate, and the entire contact zone sample was distributed unimodally about an intermediate mean.

Previous authors reported the presence of many "typical" *atricapillus* or *carolinensis* songs in contact areas (Ward and Ward 1974). Our contact zone sample also included songs that were typical in the sense that they contained two or four notes, but many of these songs were not fully typical of either parental form. For example, practically all the two-noted songs recorded in the contact zone sound to the ear and appear on a spectrogram like more or less "typical" *atricapillus* songs. Yet many of them had intermediate or even *carolinensis*-like discriminant scores (Fig. 4). Similarly, many four-noted songs, which sound like typical *carolinensis* songs, received intermediate or *atricapillus*-like discriminant scores. Thus, many contact zone vocalizations that were grossly classifiable to the human ear were nevertheless not faithful reproductions of the detailed note structure of the parental forms.

Because we did not use the number of notes per song as a variable, the discriminant analysis may have identified other, less obvious features of the songs that still characterize one or the other parental type. For instance, the discriminant weighting coefficients placed on the onset and midpoint frequencies of note 1 have similar absolute values but opposite arithmetic signs (Table 2). Essentially, the characteristic examined in this portion of the note was the difference in frequency between the two measurement points. A careful examination of the spectrograms showed that *carolinensis* reference birds tended to slur their first note, producing a major frequency change in the first half of

the note, whereas *atricapillus* notes were usually on a single frequency. Although this difference was consistent in the reference samples, it tends to break down in the contact zone (compare Fig. 3D and E). If these components were important in species recognition, the extensive intermediacy found in the contact zone would make assortative mating difficult.

Interpretation of the intermediacy found in contact zone vocalizations is complicated by the possibility of song learning (Ward and Ward 1974). Details of song ontogeny in this complex have not been worked out, but experiments by K. Apel (M. S. Ficken pers. comm.) indicate that some experience is necessary for proper development of the whistled song. *Parus atricapillus* hand-reared from the age of 15 days in isolation never produced typical "fee-bee" whistles (Ficken 1981). This suggests that learning is required for maturation of chickadee song and agrees with evidence on other *Parus* species (Becker 1978).

The possibility of song learning also makes conclusions about the extent of genetic introgression beyond the contact zone based on vocal characters hazardous. For example, one might argue that the narrowness of the zone of vocal intermediacy demonstrates that gene flow is limited. But the degree of vocal introgression expected if dispersing chickadees learn the song type of the local deme in which they finally breed is moot. Such "social adaptation" of song type is known in several well-studied species (Payne 1981). The width of any song-type transition zone will be restricted by this song-determining mechanism, because adult song type reflects not genetic constitution, but frequency of song types in the neighborhood of the birds' breeding site. The contact zone between the Mexican towhees *Pipilo ocai* and *P. erythrophthalmus*, which are well differentiated in molecular, morphological, and vocal characters, appears to display this phenomenon. The extent of vocal introgression across their contact zone is much less than introgression in molecular and morphological characters (Braun 1983).

Another consideration amplifying uncertainty as to how accurately vocal characters reflect introgression is the general tendency for female birds to disperse farther from natal to breeding site than males (Greenwood 1980). This occurs in *P. atricapillus*. Minnesota females disperse 2.34 km on average, while male dispersal averages only 1.34 km (J. Howitz pers. comm.). In Wisconsin, spring dispersal of *P. atricapillus* involves about 5% of yearling males and 9% of yearling females (Weise and Meyer 1979). Because female chickadees sing less frequently than males, a higher dispersal rate for females implies that the actual level of genetic introgression is likely to be higher than that indicated by vocal characters.

One Species or Two?

The contact zone chickadees in southwestern Missouri are intermediate in every characteristic we used to separate the two parental forms. Moreover, the distribution of variation in the contact zone is consistent with a hypothesis of panmixia. Although this evidence would be considered overwhelming in most questions of species status, two factors may engender reluctance to lump these forms. First is the tendency to believe that birds with different songs must be different species. Second, in some areas there appears to be a narrow gap between the breeding ranges of *atricapillus* and *carolinensis* (Tanner 1952, Brewer 1963, Merritt 1981).

The view that species specificity in bird song functions primarily as a reproductive isolating mechanism faces serious challenge from theories that focus on the evolutionary advantages of vocal communication to the individual. For instance, Morton (1982) suggested that singing birds may vary their songs to make it difficult for neighbors to judge their distance, thereby disrupting the neighbors' foraging activity with territorial defense. Under this hypothesis, species distinctiveness is a constraint singers face, because they must ensure that their neighbors recognize them as potential competitors. Species specificity also must be viewed in the light of information on song dialects and song learning. Regional dialects are common among sedentary bird species (Krebs and Kroodsma 1980). In fact, such dialects may exist within *P. atricapillus* (Desfayes 1964). Several examples can be cited where, like the chickadees studied here, birds do not recognize the song dialect of other conspecific populations (Thielcke 1969, Lanyon 1978). Therefore, we consider the hypothesis that *atricapillus* and *carolinensis* songs represent regional dialects of the same species a viable one.

The effect that regional dialects may have on

gene flow between avian populations is controversial (Slater 1983). Such dialects may be barriers to gene flow (Handford and Nottebohm 1976). Data have been presented to demonstrate that dialect differences in White-crowned Sparrows (*Zonotrichia leucophrys*) increase the likelihood of genetic differentiation (Baker et al. 1982), but the significance of these data has been disputed (Petrinovich et al. 1981, Zink and Barrowclough 1984, Hafner and Petersen 1985). Field studies around a contact zone between White-crowned Sparrow song dialects showed that females do not mate preferentially with males of their natal dialect (Baptista and Morton 1982), indicating that dialect is not a barrier to gene flow. In these chickadees, pair bonding occurs in the winter (Stefanski 1967, Ficken et al. 1981). The importance of the whistled song in pair bonding is uncertain (Ficken 1981). Social adaptation by males to the song dialect of their breeding deme also would diminish any obstruction dialect might present to gene flow. We see no reason to assume that chickadee song types impede gene flow at the range interface.

The mixed song repertoires of contact zone chickadees might be interpreted as a result not of hybridization but of character convergence (i.e. vocal mimicry) between competing heterospecifics (Ward and Ward 1974). We reject this vocal mimicry hypothesis in the case of chickadees because it does not predict the morphological intermediacy observed in contact zone chickadees. Merritt (1981) listed a number of instances of birds singing the songs of other species and interpreted this behavior as promoting interspecific recognition and heterospecific spacing. Several purported cases of character convergence in bird song, which also were supposed to promote heterospecific spacing, have proven illusory (Brown 1977, Murray and Hardy 1981). Furthermore, other cases of mixed song repertoires may represent inappropriate social adaptation to song types encountered at the breeding site. Practically all cases in which mixed song repertoires are common (excluding promiscuous mimics such as *Mimus*) involve closely related species; indeed, many of the species pairs hybridize (e.g. *Passerina cyanea* and *P. amoena*, Emlen et al. 1975; *Sturnella magna* and *S. neglecta*, Rohwer 1972). The songs of such closely related species may match each other's "vocal template" well enough that they are learned in the same manner as conspecific song. Observations such as those of Emlen et al. (1975) where individuals of one bunting species sang only the song of the other species are consistent with this idea. Thus, the importance of interspecific competition in producing mixed vocal repertoires remains to be demonstrated.

The second objection to the hypothesis that the two forms under consideration represent a single biological species concerns narrowly disjunct allopatry in some areas of the range interface. Brewer (1963) and Merritt (1981) reported that a narrow gap exists between the ranges of the two taxa from eastern Illinois through Indiana. Tanner (1952) noted that an elevational gap of about 180 m separates the chickadees during the breeding season in the Great Smoky Mountains. Apparently, hybridization is very limited in these areas. Brewer suggested that the Illinois-Indiana gap may act as a reproductive isolating mechanism; Tanner thought the Great Smokies elevational gap was induced competitively. While we do not dispute these vocal census data, we believe alternative explanations are equally attractive.

In our study area there were several sites where chickadees were scarce at the range interface. These sites may be analogous to the gaps observed in Illinois and Indiana. One of these areas was in Barton Co. (Fig. 1). This county has no major river system and has fewer minor drainages than do other counties in our study area. Accordingly, there is less prime riparian nesting habitat for chickadees. Chickadees were notably scarce along the range interface in Barton Co. except in abandoned strip mines that had been planted with trees. In contrast, chickadees were relatively common at the range interface in our contact zone study site (Fig. 1, Site 3). At this site, more extensive high-quality chickadee habitat exists as a result of mature woodland bordering the Osage River and several tributaries.

The sites at the range interface where we detected a lower density of chickadees may be analogous to areas where Brewer (1963) and Merritt (1981) noted gaps. Brewer (1963: 11) stated "that much of the area contained in the gap [in Illinois] does not contain vegetation optimal for chickadees." Indeed, it is evident from the maps in Brewer (1963) and Merritt (1981) that gap areas occur along the upper reaches of smaller drainages or in areas without drainage

systems. Such areas are less likely to have the mature riparian forests that are optimal for hole-nesting chickadees. Thus, when Merritt reported that chickadees withdraw from the range interface before the breeding season, he may have been observing a movement of the local populations to prime breeding habitat. This suspicion is reinforced by Merritt's (1981) spring distribution map, where almost all observations were along rivers. When coupled with the return of wintering *P. atricapillus* to northerly breeding grounds (as discussed above), this movement might have appeared quite dramatic.

It is illuminating to consider the pattern of vocal variation one might expect in areas where suitable habitat is limited at the range interface. In such areas, relatively large populations of chickadees that use the parental song types might occur to the north and south of an area where chickadees are scarce. We argued above that a chickadee dispersing to breed outside its natal deme may be able to adopt the song type of the new deme. Where suitable habitat is limited at the range interface, dispersal may be somewhat impeded, so that populations to the north and south remain fixed for the parental song types and newly arriving individuals are absorbed quickly as they adopt the local song type. Only in areas where sufficient habitat occurs would extensive vocal intermediacy be found at the range interface. The foregoing hypothesis is directly testable in gap regions, by marking fledglings and recording adult song types of birds that crossed the gap (either naturally or with the help of an investigator) to breed.

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